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REPORT

Coral–algal competition: allelopathy, temporal variance, and effects on coral microbiomes

Noam T. Altman-Kurosaki[1] · Zoe A. Pratte[2] · Frank J. Stewart[2] · Mark E. Hay[1,3]

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Abstract Seaweed–coral competition is increasingly important as reef communities degrade, with algal turfs being the most common competitor. However, experiments assessing the impacts and mechanisms involved in turf–coral competition under field conditions are rare. We evaluated turf–coral interactions and their impacts relative to those of macroalgae by placing corals (*Acropora pulchra* and *Porites rus*) in contact with turf communities from territories of two species of damselfishes, with two common macroalgae, and with inert algal mimics as physical controls. After 13 d, turfs reduced coral photosynthesis by 31–59%, while macroalgae and mimics had minimal effects. After 24 h of contact, chemicals from turf surfaces suppressed coral photosynthesis by 8–29%, affected *A. pulchra* more strongly than *P. rus*, and the significant allelopathic effects during summer were undetectable during winter. Effects of turfs on coral microbiomes were variable; contact increased microbiome richness in *A. pulchra* but had minimal impact on *P. rus* microbiomes despite photosynthesis in both corals being strongly suppressed by turfs. Thus, mechanisms driving the outcomes of turf–coral interactions include allelopathy and vary with both the coral-alga pairings involved and between seasons. If seasonal differences are due to increased temperatures, impacts of turfs on corals may strengthen as oceans warm.

Keywords Coral–turf competition · Allelopathy · Coral microbiome · Macroalgae

Introduction

Coral reefs are in global decline, shifting from coral- to algal-dominated states that provide fewer ecosystem services (e.g., Holbrook et al. 2016; Goatley et al. 2016). Understanding the mechanisms driving differential outcomes of competition between corals and algae is therefore critical for understanding changes in reef state (e.g., McCook et al. 2001; Barott et al. 2012; Adam et al. 2022). Previous work has suggested macroalgal suppression of corals via allelopathic chemicals (Rasher and Hay 2010; Bonaldo and Hay 2014; Longo and Hay 2017), promotion of coral pathogens (Smith et al. 2006), destabilization of coral's symbiotic microbiomes (Clements and Hay 2023), or shading and abrasion (Clements et al. 2020), but few studies have examined mechanisms governing outcomes of interactions between corals and turf algae.

Turf algae are ubiquitous and diverse assemblages of small, filamentous algae that are important primary producers on coral reefs and serve as the most common competitor with corals (Haas et al. 2010; Barott et al. 2012). Turfs are expected to become more common as oceans warm and acidify (Johnson et al. 2017; Anton et al. 2020). Additionally, increased sedimentation creates long-sediment laden turfs that are less productive, limit coral recruitment (Wakwella et al. 2020), and limit herbivory, reducing transfer of energy between trophic levels (Goatley et al. 2016). These various stressors have contributed

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✉ Mark E. Hay
mark.hay@biology.gatech.edu

[1] School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA

[2] Department of Microbiology & Cell Biology, Montana State University, Bozeman, MT 59717, USA

[3] Center for Microbial Dynamics and Infection, Georgia Institute of Technology, Atlanta, GA 30332, USA

to increases in turf cover and turf–coral interactions on reefs around the globe (Barott et al. 2012; Tebbett and Bellwood 2019).

Mechanisms determining the outcomes of turf–coral competition likely depend on the coral and algal species involved (McCook et al. 2001) and the ecological context in which interactions occur (Vermeij et al. 2010; Barott et al. 2012). Prior work found that turf exudates may alter coral microbiomes by "feeding" deleterious microbes at the turf–coral interfaces (Pratte et al. 2018; Roach et al. 2020) or creating zones of hypoxia that suppress the health of coral tissue (Smith et al. 2006; Brown and Carpenter 2013). These impacts are exacerbated by stressors such as sedimentation, which increases turf damage to coral tissues (Gowan et al. 2014), or by nutrient runoff, which can increase the frequency of turfs outcompeting corals (Vermeij et al. 2010). Additionally, some investigators have suggested that turfs may be allelopathic to adult corals (McCook et al. 2001; Jompa and McCook 2003), but this remains untested.

Given that turfs are variable in traits and species composition at small spatial scales (Harris et al. 2015) and that the outcomes and mechanisms of coral–algal interactions can vary depending on both the species involved and the ecological context (Rasher and Hay 2010; Barott et al. 2012; Brown et al. 2020), obtaining sufficient volumes of algal turfs with similar species composition for field manipulations is impractical. However, ecosystem engineers such as damselfishes create and defend gardens of algal turfs (Hata and Kato 2004; Ceccarelli 2007), with different species of damselfish cultivating turfs that differ in algal species composition (Ceccarelli 2007). Damselfish turfs tend to be longer, highly productive (Russ 1987), and free of sediment due to the cleaning activity of damselfishes (Tebbett et al. 2020), thus differing from common low-lying turfs. However, given that damselfish gardens: (1) can cover close to 70% of the benthos in some sites (Ceccarelli et al. 2001; Blanchette et al. 2019), (2) have become more common following removal of predators (Feeney et al. 2021), and (3) are sites in which corals often preferentially settle to escape predation (Gochfeld 2010), understanding the impact of damselfish turfs on corals is ecologically relevant and provides a tractable system to test the mechanisms impacting interactions between corals and mixed assemblages of turf algae.

Here, we utilized damselfish turfs to conduct field experiments testing whether: (i) species composition of algal turfs or the identity of the interacting coral altered turf impacts on corals, (ii) turfs impacted corals differently relative to macroalgae or inert algal mimics, (iii) turf–coral interactions were mediated by algal allelopathy, (iv) allelopathic interactions varied between warmer versus cooler periods of the year, and (v) turf contact changed coral microbiomes in a manner predictably associated with suppression of coral well-being, as prior work suggested that changes in coral microbiomes were sometimes correlated with changes in coral fitness (e.g., Krediet et al. 2013).

Methods

Study site

The study was conducted at a depth of ~ 1.5 m in the lagoon on the north shore of Mo'orea, French Polynesia (17°29′18.6″S 149°52′53.9″W). This site is protected by the seaward reef crest, experiences tidal amplitudes of < 30 cm, and consists of small patch reefs supporting corals (e.g., *Acropora* spp., *Pocillopora* spp., *Porites* spp.) and macroalgae (e.g., *Turbinaria ornata*, *Sargassum pacificum*, *Amansia rhodantha*). The territorial damselfishes *Stegastes nigricans* and *Stegastes punctatus* are common, their turf gardens differ in species composition (Ceccarelli 2007), and their territories occupy up to 68% of the benthos in some areas (Blanchette et al. 2019). *S. nigricans* constructs gardens on mounding and branching corals such as *Porites rus* and *P. lobata*, while *S. punctatus* constructs gardens on the bases of *Acropora pulchra* thickets.

Effects of algal contact on coral photosynthetic efficiency

We utilized turfs from territories of *S. nigricans* and *S. punctatus* to assess: (i) turf effects on corals, (ii) differential impacts based on turf species composition, and (iii) variance in effects on the coral *Acropora pulchra* versus *Porites rus*. Species composition of turfs in territories of *S. nigricans* versus *S. punctatus* was assessed by collecting turf haphazardly from territories ($n = 12$) of each damselfish species spread across an approximately 0.07 km^2 region in both March and September 2022. Samples from *S. nigricans* territories were collected using a 1.3-cm grommet punch and from *S. punctatus* territories by cutting a similarly sized area from territories on *A. pulchra* bases. Turfs were stored in 4% formalin in seawater, and species composition quantified following methods of Diaz-Pulido and McCook (2002) (Supplemental Methods). Differences in algal species richness were compared between damselfish species, season of collection, and their interaction using a Conway-Maxwell Poisson generalized linear model in the glmmTMB package in R (Brooks et al. 2017), as data were underdispersed. Model assumptions (i.e., normality of residuals, homogeneity of variance of residuals, and dispersion) were checked using the DHARMa package (Hartig 2022). Species cover was arcsin-square root transformed, converted to a Bray–Curtis dissimilarity matrix, and then visualized using nMDS in the vegan package (Oksanen et al. 2023). Turf communities were then compared using PERMANOVA after confirming

that the data did not violate the assumption of homogeneity of dispersions using the betadisper function in vegan.

In March 2022 (mean water temp = 28.6 °C; Leichter et al. 2023), we tested the impacts of the macroalgae *Sargassum pacificum* and *Amansia rhodantha*, turfs from *S. nigricans* or *S. punctatus* territories, plastic macroalgal mimics, turf mimics, and no-contact controls on the common corals *A. pulchra* and *P. rus* ($n = 12$ for each coral x treatment). Macroalgae were chosen due to their high abundance and differing impacts on corals (Rasher and Hay 2010; Longo and Hay 2017; Clements et al. 2020).

For our assays, seven 6–8-cm length coral fragments were collected from 12 individuals of both *A. pulchra* and *P. rus* in the study area, epoxied into the cutoff necks of plastic bottles (Z-spar Splash Zone Compound, Kop-Coat, Pittsburgh, Pennsylvania, USA—see Clements et al. 2020), and attached to inverted bottle caps secured to a metal rack ~ 20 cm above the substrate to limit abrasion from sediments (Figure S1). Treatments were assigned using a randomized block design such that each block (coral colony) had one algal treatment affixed to a different fragment from that colony, thus minimizing potential variance associated with individual colonies.

Algal treatments and mimics were applied to corals by zip-tying algae or controls directly to the corals. Turf treatments from *S. nigricans* and *S. punctatus* territories consisted of ~ 1.3 cm^2 pieces of substrate with natural turfs attached. Turf mimics (controls for effects of substrate) were substrates of similar size, sterilized in bleach, rinsed thoroughly with filtered seawater, and dried at 60 °C for 3d prior to use in the field. Macroalgal treatments were thalli ~ 6 cm in length, while controls for the physical presence alone were similar sized plastic aquarium plants resembling *Sargassum*. Prior work found that zipties and ropes used to affix algae to corals had negligible impact on corals (Rasher and Hay 2010). No-contact treatments received only zipties; we did not include a no-ziptie treatment. Cages ($5 \times 5 \times 10$ cm) of 1-cm mesh were placed over each coral to prevent consumption of corals or algae. Cages were cleaned, and all zipties, algae, and algal mimics replaced every 2 d to prevent fouling or degradation of algae.

After 13 d, treatment effects on corals were assessed via in situ pulse-amplitude-modulated (PAM) fluorometry directly at the site of coral–algal contact. PAM fluorometry quantifies the photosynthetic efficiency of coral endosymbionts (Y, or effective quantum yield)—a correlate of coral fitness. Readings for healthy corals range from ~ 0.5 to 0.7, and readings below 0.25 indicate bleaching and mortality (Fitt et al. 2001; Rasher and Hay 2010). PAM readings were conducted between 0900 and 1400 h and were blocked in time, with each block consisting of a random replicate from each coral x algal treatment, and with readings for each coral x algal treatment within a block randomly interspersed through time. Readings took 2 d, with half of the blocks being assessed each day. There were no significant differences based on date of assessment, so days were combined for further analyses. PAM readings were compared between coral species, algal treatments, and their interaction using a generalized linear mixed effects model (GLMER) using a beta family with a logit link (i.e., beta regression), as data were continuous and bounded between 0 and 1. A random effect was included to account for coral colony (1|Colony. ID). Analyses were conducted in the glmmTMB package in R (Brooks et al. 2017). Within-factor pairwise comparisons with a Bonferroni correction were made using the emmeans package in R (Lenth 2023) to assess which treatments differed within a given species of coral and to assess differential impacts of a given algal treatment between the two species of coral. Model assumptions were assessed here and below using the DHARMa package (Hartig 2022).

Treatment effects on coral microbiomes were assessed via collecting a fragment from the region of coral-treatment contact after taking PAM readings following Clements et al. (2020). Samples were crushed, placed in RNALater (ThermoFisher Scientific), and stored at − 80 °C until analyzed (see below). All sampling tools were rinsed thoroughly in seawater between samples to minimize contamination. While these methods are not aseptic, prior work has found they are sufficient for identifying among-treatment differences in microbiomes for field-based studies (Pratte et al. 2018; Clements et al. 2020, 2024).

Effects of turf surface chemicals on coral photosynthesis

In March 2022, we tested for algal allelopathy by extracting the surface chemicals from both turf communities using methods of De Nys et al. (1998). Twenty milliliter volumes of turf algae collected from *S. nigricans* or *S. punctatus* territories were spun for 30 s in a mesh bag and blotted with paper towels to remove excess water. Algae were then vortexed for 30 s in 50 mL of hexane. The hexane was then decanted into a tube, which was then placed in a fume hood for 8.5 h to evaporate off the hexane, leaving the lipid-soluble surface extracts. Surface extracts from each turf type were separately resuspended in 1 mL of methanol before being added to phytagel strips following the methods outlined in Rasher and Hay (2010). Five hundred microliters of the methanol/extract mix was stirred with 9.5 mL of heated water and 220 mg of phytagel (Sigma-Aldrich, USA) and poured into a mold over a window screen and cut into $1 \times 1 \times 0.1$ cm strips. Control strips were made with 500 µL of methanol but no algal extract. Strips were refrigerated for less than 12 h prior to deployment in the field.

Effects of extracts were assessed in situ by zip-tying phytagel strips directly to fragments of *A. pulchra* and *P.*

rus for 24 h in the field. New coral fragments were collected, placed on racks, and blocked by colony (as above) so that a control strip and strips with extracts from each turf type were blocked by individual coral colony for each of the two coral species ($n = 12$ blocks per treatment). Treatment effects on photosynthetic efficiency were measured after 24 h using PAM fluorometry, with assessments conducted between 0900 and 1400 h. PAM readings were compared between coral x algal treatments using beta regression with coral colony ID as a random effect as above.

Allelopathy can vary across seasons (Oliveira et al. 2022), as can outcomes of coral–algal interactions (Brown et al. 2020). We hypothesized that seasonal outcomes of coral–algal interactions could be due to seasonal variance in the production of allelochemicals by algae or resistance to those chemicals by corals. Given this, the surface extract assay was repeated with newly collected coral fragments in September 25–28, 2022, when temperatures averaged 26.3 °C (i.e., 2.3 °C cooler than during the March experiments). To account for differences in turf allelopathy due to seasonal changes, we tested the allelopathy of turf extracts from turf that we collected in September versus extracts from turf that we had collected in March and preserved at − 80 °C. If extracts from turf that we collected in March had a reduced effect in September and/or if extracts from turf that we collected in September had a lower impact on corals relative to the March turf, then this could suggest that allelopathic effects of turfs on corals are reduced in winter months. PAM readings were compared between coral species x treatments using beta regression with coral colony ID as a random effect as above.

Sampling and analysis of effects on coral microbiomes

We assessed the composition of coral microbiomes from treatments in the initial coral–algal contact experiment using Illumina sequencing of PCR amplicons spanning the V4 region of the prokaryotic 16S rRNA gene. We extracted the total DNA from each coral fragment using the DNeasy Powersoil Pro DNA Extraction Kit (Qiagen) following manufacturer's instructions and quantified dsDNA following extraction using a Qubit fluorometer. Two blank extractions were performed without any samples as a quality control measure. The V4 region of the 16S rRNA gene was sequenced using standard Illumina amplicon protocols. Amplicons were generated with a two-step PCR approach. The first PCR amplified the V4 region using primers 515F (Parada) (5′-GTGYCAGCMGCCGCGGTAA-3′) and 806R (Apprill) (5′-GGACTACNVGGGTWTCTAAT-3′), each with an Illumina adapter overhang. The second PCR appended Illumina barcodes and adapters to the amplicons. PCR conditions are given in the supplemental material. Amplicons were sequenced on an Illumina MiSeq using 250 × 250 V2 chemistry with 20% PhiX at the ME Core at Georgia Tech.

Barcoded sequence reads were screened for length, quality, and chimeras in QIIME 2 (version 2023.2) using DADA2 (Callahan et al. 2016). Taxonomy was then assigned using the SILVA database (version 138). Contaminants were removed following the methods used in (Pratte et al. 2018; Clements et al. 2020, 2024). Briefly, we averaged all ASVs found in samples and all ASVs found in blanks. All amplicon sequence variants (ASVs) that were relatively more abundant on average in the blanks compared to the coral samples were removed as contaminants. All ASVs that were classified as mitochondria or chloroplast or did not classify as bacteria or archaea were also removed. Four ASV tables were created, one rarefied table to the minimum number of reads in the cleaned table (4798) and one unrarefied table for each species of coral. All blanks were removed by the QC and rarefaction process. All analyses after this point were conducted independently for *P. rus* and *A. pulchra*. The rarefied ASV tables for each species were imported into R for all diversity analyses, while the unrarefied table was imported into R for DESeq2 analysis (Love et al. 2014) to detect which microbial taxa differed significantly between treatments for each coral species.

We assessed treatment effects on microbial alpha diversity in *A. pulchra* and *P. rus* with generalized linear mixed effects models with a random effect to account for coral parent colony ID using the lme4 and glmer.nb packages in R. Microbial species richness (observed ASVs) for *P. rus* was compared using a Poisson regression model, while comparisons for *A. pulchra* were made using a negative binomial model to account for overdispersion and heteroskedasticity of the residuals. Treatment effects on Shannon diversity for both corals were compared using gamma regression with a log link as data were positive, continuous, and right skewed.

We analyzed treatment effects on beta diversity by converting ASV counts to relative abundances and square root transforming them prior to constructing a Bray–Curtis dissimilarity matrix. Differences in microbial community composition were visualized with a principal coordinates analysis (PCoA) and compared between treatments with PERMANOVA using the vegan package (Oksanen et al. 2023). Pairwise-PERMANOVA tests with a Bonferroni correction were run post hoc to test for significant differences between treatments. Beta dispersion (i.e., multivariate homogeneity of variance) for both dissimilarity matrices was calculated using the betadisper function and compared between treatments using a permutation test using the vegan package in R (Oksanen et al. 2023). Preliminary data visualization suggested that rare species comprised a large proportion of the microbiomes of both species of coral. As such, we also assessed treatment effects on beta diversity and beta dispersion calculated

using a binary Jaccard matrix that equally weights rare and common species, which can be found in the supplements (Figure S3, Table S3).

Results

Differences in turf species composition

Turf species composition and relative abundance varied significantly based on the interaction between damselfish species and season (Fig. 1, PERMANOVA, $R^2 = 0.03$, $F = 3.5$, $P = 0.02$). In particular, there were marked differences in the community composition of turfs between damselfishes regardless of season (PERMANOVA, $R^2 = 0.53$, $F = 59.1$, $P < 0.01$), but strong seasonal differences in turf composition were apparent only for *S. punctatus* based on the nMDS ordination. However, turfs did not differ in species richness as a function of damselfish species (Figure S2, GLM, $\chi^2 = 3.3$, $P = 0.07$), season ($\chi^2 = 0.75$, $P = 0.38$), or the interaction of these two factors ($\chi^2 = 2.1$, $P = 0.14$). A description of species shifts, a list of all species, and their relative abundances are given in Supplemental Tables S1 and S2.

Effects of algal contact on coral photosynthetic efficiency

Coral effective quantum yield varied significantly based on the interaction between algal treatment and coral species (Fig. 2, GLMER, $R^2_m = 0.85$, $R^2_C = 0.86$, $\chi^2 = 24.3$, $P < 0.01$), driven by a stronger impact of both turfs on the photosynthesis of *P. rus* (~ 45–60% suppression of photosynthesis) relative to *A. pulchra* (~ 30–35% suppression of photosynthesis; emmeans, *S. nigricans:* z-ratio = 2.9, $P < 0.01$; *S. punctatus*: z-ratio = 4.5, $P < 0.01$). The effect of *Sargassum* on photosynthetic yield did not differ from controls, macroalgal mimics, or turf mimics for either coral species (Fig. 2, Table S4). *Amansia* suppressed photosynthesis of *P. rus* ~ 15–19% relative to controls, but did not significantly suppress photosynthesis of *A. pulchra*. *S. nigricans* turf suppressed the photosynthesis of *P. rus* by ~ 45–48% relative to controls and by ~ 36% and ~ 30% more than the effects of *Sargassum* or *Amansia*, respectively (Fig. 2, Table S4). *S. nigricans* turf suppressed the photosynthesis of *A. pulchra* by ~ 30–32% relative to controls and ~ 17% more

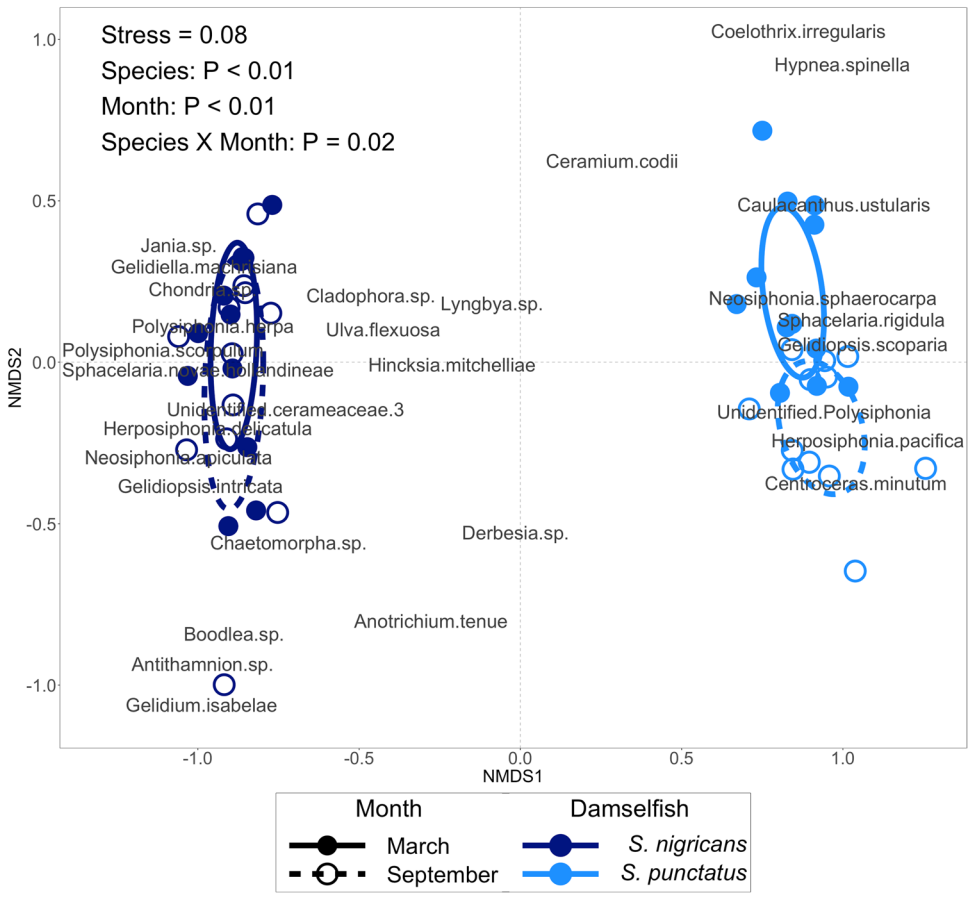


Fig. 1 Community composition of turfs collected from *S. nigricans* and *S. punctatus* territories during March and September. Multivariate comparison of turf community composition is via an nMDS plot of arcsin-square root-transformed turf species cover. Ellipses represent 95% confidence intervals of turf community composition for each damselfish species in each season. Species labels represent the mean centroid for each species in the turf species matrix. P-values are from a PERMANOVA

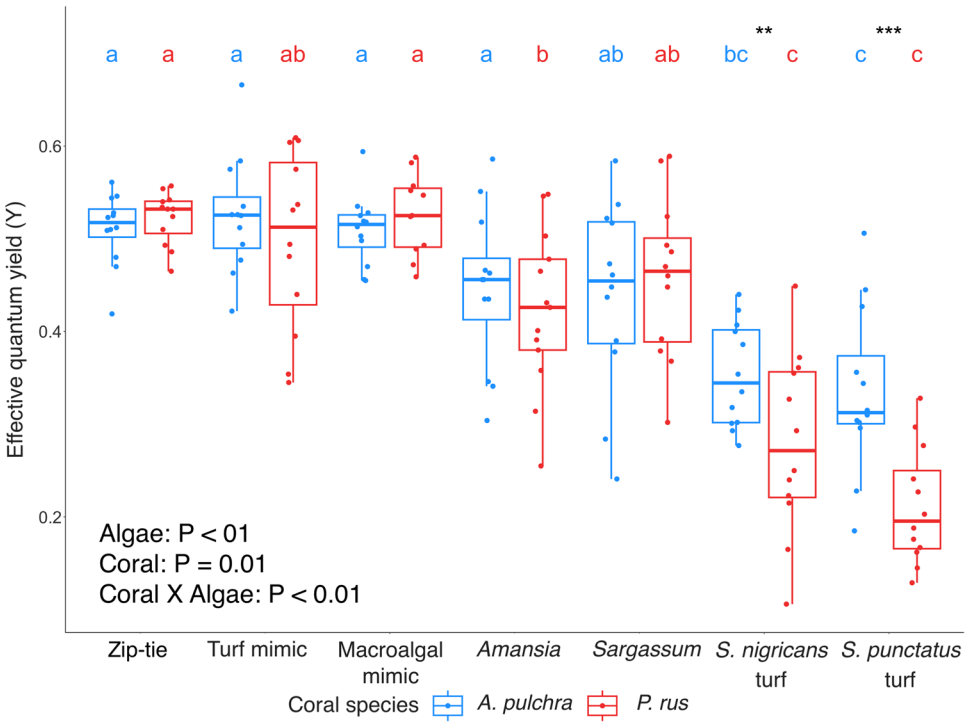


Fig. 2 Coral photosynthetic efficiency after 13 d of algal contact. Boxplots show *Acropora pulchra* (blue) and *Porites rus* (red). Points outside of whiskers indicate outliers (i.e., 1.5*IQR). Letters denote significant differences among treatments within each coral species (emmeans comparisons, $P < 0.05$). Stars indicate a significant difference in the impact of an algal treatment between coral species (emmeans comparisons, ** $P < 0.01$, *** $P < 0.001$)

than the effects of *Amansia*, but suppression did not differ significantly from the effects of *Sargassum* (emmeans, z-ratio = −2.8, $P = 0.10$). Finally, *S. punctatus* turf impacted both corals more than any control or macroalgal treatment, suppressing *P. rus* photosynthesis by 57–69% relative to the three controls and by 49–53% relative to the two macroalgae (Table S4). It suppressed *A. pulchra* photosynthesis by ~ 34–36% relative to controls and by ~ 25–27% relative to the two macroalgae (Fig. 2, Table S4).

Effects of turf surface extracts on coral photosynthesis

Tests of turf surface extracts on coral photosynthesis demonstrated a significant interaction between coral species and algal extracts (Fig. 3, GLMER, $R^2_m = 0.75$, $R^2_C = 0.82$, $\chi^2 = 13.1$, $P < 0.01$), with extracts producing greater impacts on *A. pulchra* relative to *P. rus*. Surface extracts from *S. nigricans* turf reduced photosynthesis of *A. pulchra* by a significant ~ 26% relative to the control, while this extract did not significantly reduce the photosynthesis of *P. rus* (Table S5). Extracts from *S. puncatus* turfs significantly suppressed the photosynthesis of both *P. rus* and *A. pulchra*, by 12% and 13%, respectively. Extracts from *S. nigricans* and *S. punctatus* turfs suppressed photosynthesis of *A. pulchra* by 17% and 16% more than they did *P. rus*, respectively (Fig. 3, Table S5).

Turf extracts did not suppress coral photosynthesis in September when water temperature averaged 26.3 °C (2.3 °C cooler than the assays in March; Fig. 4, GLMER, $R^2_m = 0.36$, $R^2_C = 0.57$, $\chi^2 = 6.1$, $P = 0.19$). In this assay, there was a significant effect of coral species ($\chi^2 = 8.1$, $P < 0.01$), with *A. pulchra* having a lower photosynthesis than *P. rus* regardless of treatment, but no algal surface extract caused a significant reduction in photosynthetic efficiency relative to controls during this September experiment (Table S6).

Treatment effects on coral microbiomes at sites of contact

Sequence reads ranged from 30,694 to 128,524 per sample, with an average of 72,273. 81.47% of these reads passed merging, denoising, and chimera checks. Blank samples only had 542 and 763 reads, half of which did not pass quality control. 773 ASVs were removed (out of a total of 23,559). All but one of these contaminant ASVs contributed less that 0.3% relative abundance to the entire dataset before filtering, and the one ASV contributed 13.7%, and only identified as "bacteria," suggesting it might be mitochondrial contamination. From the cleaned ASV table, samples ranged from 4798 to 16,922 reads. Gammaproteobacteria were abundant in both coral species, but *A pulchra* was primarily dominated by Gammaproteobacteria and Chlamydiae, while *P. rus* was more evenly distributed among Gammaproteobacteria, Bacteroidia, Alphaproteobacteria, and Cyanobacteria (Figure S4).

Coral microbiome composition differed significantly among treatments for both coral species. The effect was

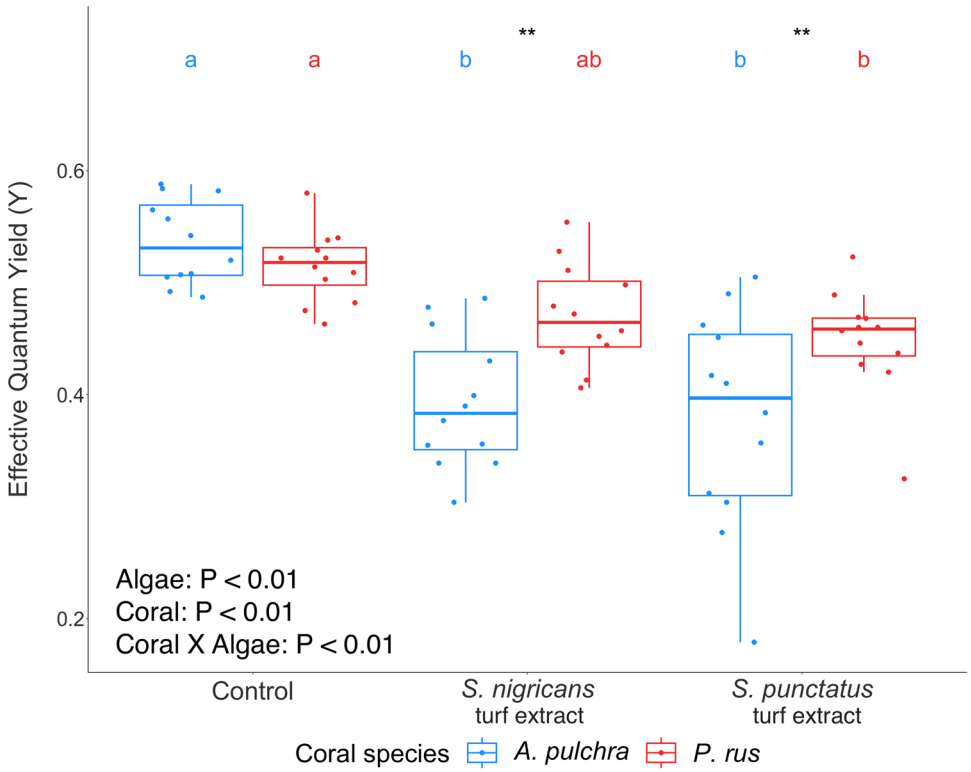


Fig. 3 Effects of turf surface extracts on coral photosynthetic efficiency after 24 h of exposure during the Austral summer. Boxplots, colors, points, stars, and letters are as in Fig. 2

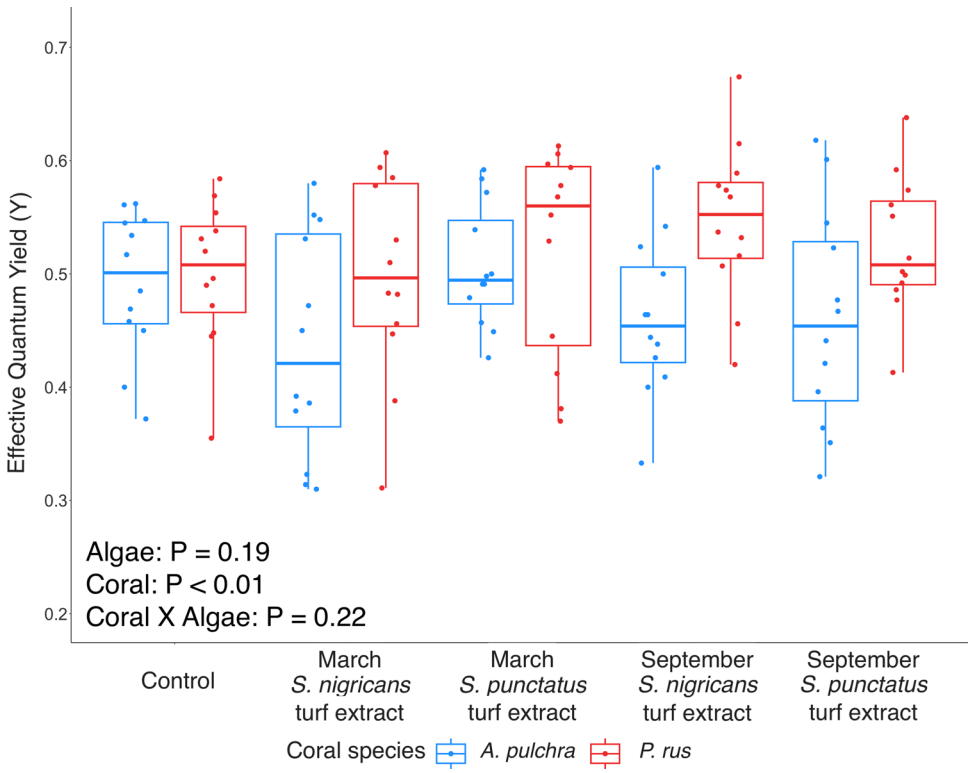
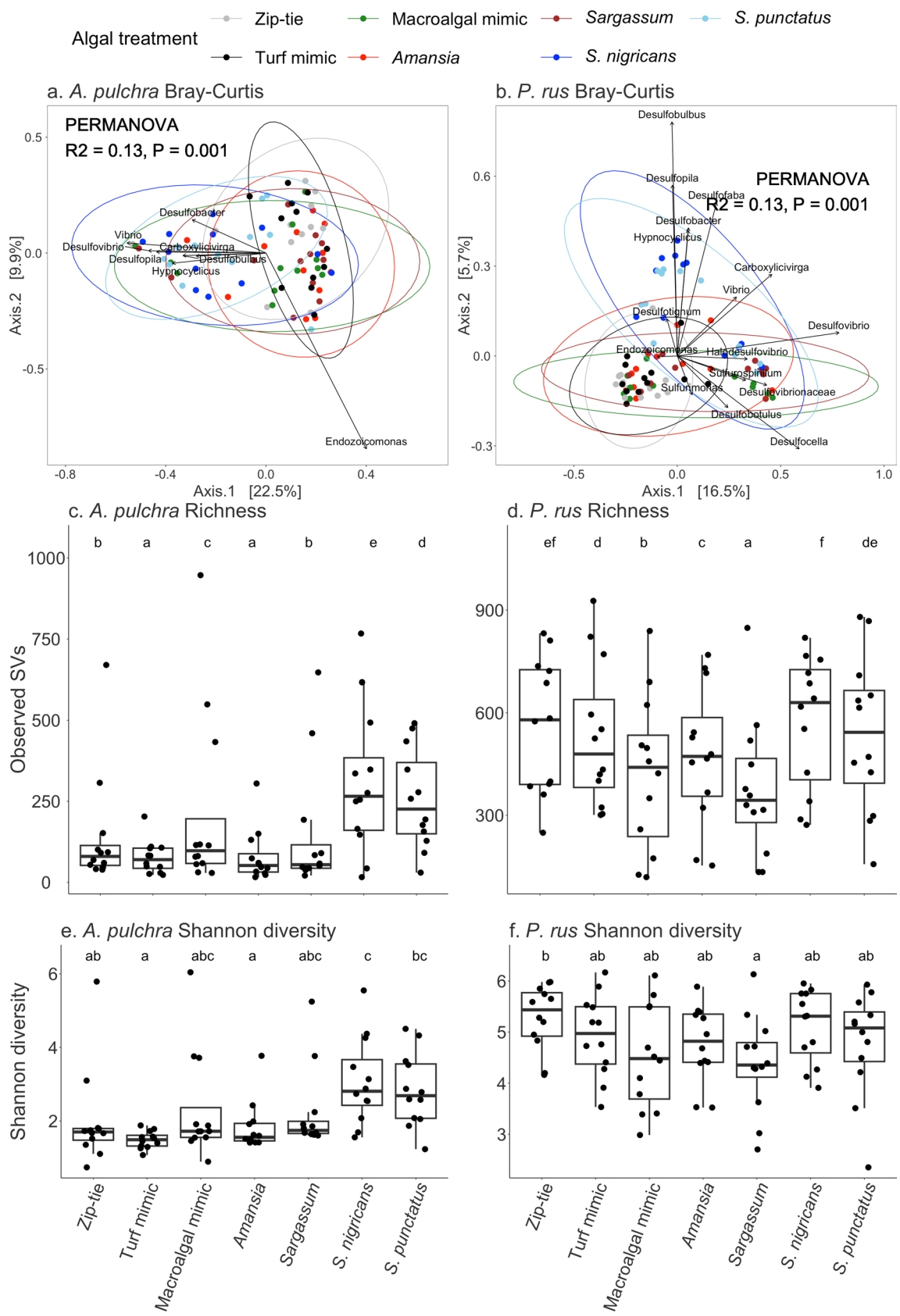


Fig. 4 Photosynthetic efficiency of corals in the austral winter when exposed to extracts of turfs collected in March and September for 24 h. Boxplots, colors, points, stars, and letters are as in Fig. 2. There were no significant differences among treatments within a coral species (emmeans comparisons)

strongest for *A. pulchra* (Fig. 5a, PERMANOVA, $R^2 = 0.13$, $F = 2.1$, $P < 0.01$), with microbiomes of corals in contact with either of the turf treatments distinct from those in contact with turf mimics, and those in contact with *S. punctatus* turf different from zip-tie only controls (Table S3, pairwise-PERMANOVA, $P < 0.05$). Beta dispersion did not


Algal treatment
Zip-tie
Turf mimic
Macroalgal mimic
Amansia
Sargassum
S. nigricans
S. punctatus
a. A. pulchra Bray-Curtis
PERMANOVA
R2 = 0.13, P = 0.001
Axis.2 [9.9%]
Axis.1 [22.5%]
Desulfobacter
Vibrio
Desulfovibrio
Carboxylicivirga
Desulfopila
Desulfobulbus
Hypnocyclicus
Endozoicomonas
b. P. rus Bray-Curtis
PERMANOVA
R2 = 0.13, P = 0.001
Axis.2 [5.7%]
Axis.1 [16.5%]
Desulfobulbus
Desulfopila
Desulfofaba
Desulfobacter
Hypnocyclicus
Carboxylicivirga
Vibrio
Desulfotignum
Desulfovibrio
Endozoicomonas
Halodesulfovibrio
Sulfurospirillum
Sulfurimonas
Desulfovibrionaceae
Desulfobotulus
Desulfocella
c. A. pulchra Richness
Observed SVs
b a c a b e d
d. P. rus Richness
ef d b c a f de
e. A. pulchra Shannon diversity
Shannon diversity
ab a abc a abc c bc
f. P. rus Shannon diversity
b ab ab ab a ab ab
Zip-tie
Turf mimic
Macroalgal mimic
Amansia
Sargassum
S. nigricans
S. punctatus

◂**Fig. 5** Treatment effects on a&b) microbiome composition (beta diversity), c&d) richness, and e&f) Shannon diversity of *A. pulchra* and *P. rus*, respectively. Color in a&b denotes algal treatment; ellipses represent 95% confidence intervals; vectors indicate microbial taxa of interest as identified by DeSeq analysis; % values in brackets indicate the variance explained by a given principal coordinate axis. For c-f, points outside of whiskers on boxplots indicate outliers (i.e., 1.5*IQR); letters denote significant groupings (emmeans comparisons, $P < 0.05$)

differ among treatments in *A. pulchra* (Permutation test, $F = 1.8$, $P = 0.11$). Results for *P. rus* were similar; there was a significant treatment effect (Fig. 5b, PERMANOVA, $R^2 = 0.13$, $F = 1.9$, $P < 0.01$), with microbiomes of corals contacting *S. nigricans* or *S. punctatus* turf distinct from those contacting turf mimics or zip-tie only controls (Table S3, pairwise-PERMANOVA, $P < 0.05$), and microbiomes of corals in contact with *S. nigricans* turf differing from those in contact with *Amansia* (Table S3, pairwise-PERMANOVA, $P < 0.05$). As with *A. pulchra*, beta dispersion did not differ among treatments (Permutation test, $F = 0.82$, $P = 0.55$).

Microbial richness and diversity differed significantly among treatments for both corals (Fig. 5c-f). *A. pulchra* microbiomes exposed to turfs had higher richness than all other treatments (Fig. 5c; $P < 0.05$). However, Shannon diversity of *A. pulchra* fragments in contact with *S. nigricans* turf did not differ from those in contact with *Sargassum* (z-ratio = 1.9, $P = 0.57$), or macroalgal mimics (z-ratio = − 2.1, $P = 0.36$), and Shannon diversity of corals in contact with *S. punctatus* turf did not differ from those in contact with zip-tie only controls (Fig. 5e, z-ratio = − 2.6, $P = 0.12$). For *P. rus*, microbial richness and Shannon diversity differed among treatments, but differences did not parallel those in *A. pulchra* (Figs. 5d,f). Microbial richness did not differ among *S. punctatus* turf, turf mimics, or zip-tie only control treatments (Fig. 5d, $P > 0.05$), nor was there a difference between *S. nigricans* turf and zip-tie only controls (z-ratio = − 1.2, $P = 0.87$). The only difference in Shannon diversity was that the *Sargassum* treatment had lower diversity than zip-tie only controls (Fig. 5f, emmeans, z-ratio = 3.1, $P = 0.04$). Overall, treatment-associated changes in microbiomes did not consistently coincide with treatment effects on coral photosynthesis. For *A. pulchra*, turf contact suppressed coral photosynthesis and increased microbial diversity, but for *P. rus*, even though turf contact suppressed photosynthesis more strongly, it did not enhance microbial diversity relative to controls.

DESeq2 analysis identified 105 microbial genera that varied among treatments, with pairwise tests involving either of the turf treatments resulting in the most differentially abundant microbial taxa (Figure S5). Five and 13 of these genera in *A. pulchra* and *P. rus*, respectively, were associated with sulfate reduction and sulfur cycling (e.g., *Desulfotignum*; Saad et al. 2017; Reyes-Sosa et al. 2018), although trends were inconsistent among treatments (Fig. 5a, b; Table S7). *A. pulchra* tended to be dominated by *Endozoicomonas* (mean relative abundance ± SE = 62 ± 3% of reads) in all fragments not contacting turf, with turf contact reducing *Endozoicomonas* read abundance by ~ 22%. *Endozoicomonas* was significantly depressed in treatments where *A. pulchra* contacted *S. nigricans* turf relative to all other treatments (Table S7, $P < 0.01$), and in those contacting *S. punctatus* turf relative to *Sargassum* and macroalgal mimics (Table S7, $P < 0.01$). *Vibrio* was often elevated in both *A. pulchra* and *P. rus* contacting turf and macroalgae relative to controls (Table S7, $P < 0.01$). *Vibrio* relative abundance never exceeded 3% in *Porites* fragments in the zip-tie control treatment or 6% in the turf mimic treatments but reached up to 16% and 13% in treatments in contact with *S. nigricans* turf and *S. punctatus* turf, respectively. In contrast, mean relative abundance of *Vibrio* never exceeded 1% regardless of treatment for *A. pulchra*, and there was no difference in *Vibrio* abundance between turf treatments and macroalgal treatments for *A. pulchra* (Table S7, $P > 0.05$). *Carboxylicivirga*, an anaerobic microbe that could indicate hypoxic conditions (Wang et al. 2015; Cai et al. 2021), was elevated in both *A. pulchra* and *P. rus* fragments that were in contact with either turfs or *Sargassum* relative to other treatments (Table S7, $P < 0.01$), although relative abundance never exceeds 1% or 4% for *A. pulchra* or *P. rus*, respectively. A complete list of changes in microbial genera between treatments and effect sizes can be found in Table S7.

Discussion

Corals and turf algae are commonly the most frequent competitors on coral reefs (Barott et al. 2012). Factors such as eutrophication (Vermeij et al. 2010) and increased sedimentation (Gowan et al. 2014; Tebbett and Bellwood 2019) can result in turfs winning more interactions with corals, increasing coral tissue damage (Gowan et al. 2014). While most manipulative research on coral–algal competition has focused on macroalgae as opposed to turfs (Rasher and Hay 2010; Clements et al. 2020), a growing body of work suggests that turf dominance—not macroalgae dominance—will be more characteristic of degraded and future reefs (O'Brien and Scheibling 2018; Tebbett and Bellwood 2019). The dynamics and mechanisms affecting coral–turf interactions may therefore be especially important in determining whether reefs recover or continue to degrade following disturbances (Adam et al. 2022). Here, we utilized more easily manipulated turfs from damselfish territories to examine mechanisms driving the outcomes of coral–turf competition and found: (i) that turfs can have a larger impact on corals than common

species of macroalgae, (ii) that extracts from turf surfaces can produce harmful chemical effects, (iii) that algal allelopathy can vary with season, (iv) that turf impacts on coral microbiomes vary between coral species, and (v) that changes in coral microbiomes are not consistently associated with suppression of coral photosynthesis.

Contact with turf communities from the territories of two species of damselfish significantly reduced the photosynthetic efficiency of two corals that are commonly associated with damselfish territories, and this effect was usually greater than that of common macroalgae. Thus, coral–algal interactions are dependent on both the coral and algal species involved and turfs can actively damage corals and hasten reef decline, as suggested by previous studies (Haas et al. 2010). However, while contact with algae from both communities of turf significantly reduced *P. rus* photosynthesis, extracts from *S. nigricans* turf did not significantly suppress *P. rus* photosynthesis. This species of damselfish often creates turf gardens on *P. rus* (Blanchette et al. 2019), so it is possible that *P. rus* has acclimated to the chemicals from these turfs, but is not able to compensate for other stressors associated with live turf, such as increases in pathogens (Nugues et al. 2004; Pratte et al. 2018) or hypoxia (Brown and Carpenter 2013). Our observation of increased *Vibrio* (Ben-Haim and Rosenberg 2002) and *Carboxylicivirga* (Wang et al. 2015; Cai et al. 2021) is consistent with this, although overall impacts on the *P. rus* microbiome due to turf contact were unclear. Regardless, these results suggest that the mechanisms by which turfs damage corals likely depend on the species involved.

Multiple studies indicate that lipid-soluble compounds on seaweed surfaces commonly mediate allelopathic interactions between algae and corals (Rasher and Hay 2010; Andras et al. 2012; Longo and Hay 2017; Clements et al. 2020), and allelopathy has been hypothesized as a mechanism by which turfs can damage corals (McCook et al. 2001; Jompa and McCook 2003). However, allelopathy of turfs had never been explicitly tested, possibly due to the difficulty of collecting adequate quantities of sparse turfs, or to species differences in diverse turf assemblages potentially producing variable chemical effects (Harris et al. 2015). During the austral summer, lipid-soluble surface extracts from both turf communities reduced photosynthetic efficiency of *A. pulchra,* and extracts from *S. punctatus* turfs suppressed photosynthesis of *P. rus*. Turf extracts were not suppressive for either coral during the austral winter. This could indicate that corals are more susceptible to allelochemicals during warmer months, similar to how corals may become more susceptible to pathogens during periods of elevated temperatures (Ben-Haim et al. 2003). However, there was substantially more variance between colonies in their response to turf extracts in the September experiment, where the random effects explained 21% of the variance in the data as opposed to 7% in the March experiment. Thus, colonies may vary more in resistance to turf chemicals during winter months.

Our findings of seasonal variance in allelopathic effects, that corals differ in susceptibility to turf allelopathy, and that allelopathic potency varies between turfs of differing species composition might explain the variable outcomes of turf–coral interactions observed across both local and broader geographic gradients (Barott et al. 2012; Haas et al. 2010). Prior studies have found that allelopathy assays like these produce similar effects to placing live algae in direct contact with corals (e.g., Rasher and Hay 2010) and that known allelopathic metabolites occur on algal surfaces where they can be transferred to corals upon contact (Andras et al. 2012), but we did not isolate and identify the responsible compounds and thus cannot quantify their presence and concentration on algal surfaces. Future studies identifying the active compounds and quantifying their concentrations on algal surfaces would be valuable. Additionally, hydrophilic extracts from some algae can suppress coral settlement (Evensen et al. 2019) and can promote microbes in groups suggested to be coral pathogens (Morrow et al. 2017), so studies on the effect of water-soluble chemicals from damselfish turfs would also be useful.

A prior study by Brown et al. (2020) found that outcomes of coral–algal interactions varied seasonally, with macroalgae causing the least damage to corals during the summer—when our surface extracts had greater impact—and turf algae tending to win interactions regardless of the season. However, they did not assess the mechanisms driving seasonal variance in competitive outcomes. Our results suggest that coral susceptibility to allelochemicals and/or turf production of allelochemicals varies seasonally, with greater effects during warmer periods. While few studies have examined the mechanisms that underlie seasonal variance in allelopathy on coral reefs, seasonal warming can enhance the production of allelochemicals and competitively favor species involved with algal blooms (Wu et al. 2017) and increases the invasiveness of some corals (Oliveira et al. 2022) and shrubs (Medina-Villar et al. 2020). It is therefore possible that turf extracts were more potent in the summer due to enhanced production of allelochemicals. However, if this were the case, we would have expected our March extracts to have a similar impact on corals during the September experiment. While our reliance on turf that we had collected and frozen (thus lysing some cells) in March for the seasonal component of this experiment likely resulted in the extraction of some internal lipid-soluble chemicals along with the surface lipid-soluble chemicals, this should have enhanced the effect of chemicals on corals, as opposed to diminishing it. It is plausible that the differences in our results are due to increased coral susceptibility to turf surface chemicals during the warmer months or that the active metabolites degrade over time even when frozen (Cronin

et al. 1995). Our observation that lipophilic extracts did not reduce coral photosynthesis when water was cooler suggests that chemically mediated suppression of corals by turf algae may increase as oceans continue to warm.

Several authors have suggested that algae disrupt coral microbiomes via release of dissolved organic carbon (see Clements and Hay 2023 for an overview), and we had hypothesized that algal impacts on coral microbiomes would be reflected by their impacts on coral photosynthesis, as prior work has found that shifts in coral microbiomes due to algal contact can be correlated with reduced growth (Krediet et al. 2013). However, we found that turf impacts on coral microbiomes did not consistently differ from effects due to turf controls, macroalgae, or inert macroalgal mimics. While turf contact increased microbial species richness and diversity for *A. pulchra*—potentially indicating dysbiosis and reduced health (Zaneveld et al. 2017; Beatty et al. 2019)—it had little to no effect on *P. rus* microbiomes, despite photosynthesis of *P. rus* being more strongly suppressed by turf contact.

Differences in turf impacts on coral microbiomes could be due to intrinsic differences in these corals. For example, while changes in microbial diversity can indicate dysbiosis in some corals (Zaneveld et al. 2017; Beatty et al. 2019), more diverse microbiomes can also be more resistant to disease (Pollock et al. 2019). *P. rus* microbial communities were generally more diverse and more even than *A. pulchra*'s, including more classes of microbes. This increased diversity and evenness might have increased *P. rus* microbial stability. In contrast, *A. pulchra*'s microbiome was dominated by Gammaproteobacteria, such as *Endozoicomonas* and Chlamydiae. Recent work has found that some members of Chlamydiae such as *Simkania* depend on the by-products of *Endozoicomonas* for functioning (Maire et al. 2023) and the importance of *Endozoicomonas* in *A. pulchra* health and immune function has been documented (Ezzat et al. 2021), so the significant depression of *Endozoicomonas* by turf could have contributed to the reduced stability of the *A. pulchra* microbiome and could indicate increased susceptibility to disease.

For both corals, turf and macroalgal treatments led to increases in *Vibrio* relative to controls; such shifts are often associated with bleaching and disease (Ben-Haim et al. 2003; Sweet et al. 2013) and have been observed in coral microbiomes from algal vs. coral-dominated reefs (Beatty et al. 2019). Turf treatments also often led to shifts in the abundance of microbial genera associated with sulfur cycling, the by-products of which are important nutrient sources for both coral pathogens and coral-associated bacteria (Raina et al. 2010; Garren et al. 2014). Turf contact also enhanced *Carboxylicivirga* (Wang et al. 2015; Cai et al. 2021), an anaerobic microbe that could indicate hypoxic conditions at the turf–coral interface. It is possible that these changes reflect coral microbiomes becoming more similar to algal microbiomes, potentially due to crossover of microbial taxa through direct contact (Pratte et al. 2018). We did not assess algal microbial communities in this experiment, and these effects would be worth examining further. Regardless, our results suggest that turf contact shifts microbiomes of some corals (*A. pulchra*) more than others (*P. rus*).

Although the photosynthesis of *P. rus* was more strongly suppressed by turf contact than the photosynthesis of *A. pulchra*, effects of algal extracts and changes in the microbiome of *P. rus* were modest. It is possible that chemically and microbially mediated mechanisms act synergistically to damage corals, although we did not test this explicitly and synergisms between multiple mechanisms of competition warrant further investigation. It is also possible that mechanisms such as zones of reduced oxygen at the coral–turf interface (Smith et al. 2006; Brown and Carpenter 2013), or other turf traits contributed to the reduced photosynthesis of *P. rus* in the algal contact as opposed to extract treatments. Because Acroporids face elevated extinction risk due to warming (Carpenter et al. 2008), whereas *P. rus* is relatively hardy (Lenz and Edmunds 2017), increased susceptibility of *P. rus* to turf competition is worrisome in that it may accelerate the decline of even the hardier corals.

Given that turfs are favored by factors associated with coastal development (e.g., Vermeij et al. 2010; Gowan et al. 2014) and by future ocean conditions (Johnson et al. 2017; Anton et al. 2020), understanding the mechanisms and dynamics underlying turf–coral interactions is of increasing importance. Our results suggest that the mechanisms driving the outcome of coral–turf competition are context dependent, can differ depending on both the coral and algal species involved, and may vary with the season or temperature in which that interaction occurs. Turfs can suppress corals via allelopathy and changes in coral microbiomes co-occur with turf contact for some corals. If these differences in microbiomes include shifts in pathogen abundance or activity, this could account for variance among coral species in coral recovery following algal contact (Bonaldo and Hay 2014). Increased susceptibility of corals to turf surface chemicals during summer months may act in tandem with microbially mediated competition, such as increased susceptibility of corals to disease during summer months and periods of extreme heat (Ben-Haim et al. 2003; Howells et al. 2020). Given continued ocean warming, these synergisms and context dependencies of coral–algal competition warrant further investigation for improved management of imperiled reefs in the Anthropocene.

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Author contributions NTAK and MEH designed the experiment. NTAK collected the data. NTAK and ZFP conducted data analysis and generated figures. All authors contributed to writing, read, and approved the completed manuscript.

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Data availability Datasets used in this study are currently being processed within the BCO-DMO data system and will be available online (http://bco-dmo.org/) upon manuscript acceptance. Datasets and code are presently available at github: https://github.com/naltmank/coral_turf_contact_exp. Raw sequence data are publicly available at NCBI's SRA Database under BioProject PRJNA1037572.

Declarations

Conflict of interest The authors declare no competing interests relevant to the content of this article.

Ethical approval Permit for research was granted by the French Polynesian Government (Délégation à la Recherche) and Haut-commissariat de la République en Polynésie Française (DTRT) under research permit Protocole d'Accueil 2022. Corals were transported under CITES permit number FR2298700091-E.

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